Past forests of Europe

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European forests have varied in their composition, structure, and extent over the last 5 million years or more in response to global climate changes. European forests have also undergone very major changes due to the alternating glacial-interglacial cycles of the Quaternary (last 2.6 million years). European forests have greatly changed in their extent and structure in the last 5 000 years due to human activities (the *Homo sapiens* phase) in the current Holocene interglacial in which we live. Contemporary ecologists and foresters can learn from 'lessons from the past' about forest responses and resilience to environmental changes in the past.

Introduction

Were European forests 500, 5 000, 15 000, 150 000, 1.5 million, 2.5 million, and 5 million years ago similar in species composition, structure, and extent to the forests of Europe today? As we cannot directly observe the forests of the past, to answer these questions we need to reconstruct past forests indirectly using the fossil record. This involves the study of seeds, fruits, leaves, wood, and charcoal (macrofossils)[1] and of microscopic pollen grains, spores, cells (e.g. stomata), and charred particles (microfossils) preserved in lake, bog, alluvial, and other sediments where organic material can be preserved[2]. Pollen analysis as a tool for vegetation reconstruction - invented in 1916 by the Swedish geologist Lennart von Post - was and still is the dominant technique in the Quaternary period, especially the last 15 000 years of the late-Quaternary. Von Post had the idea of expressing fossil pollen assemblages as percentages of the sum of pollen grains counted, and of presenting these percentages as stratigraphical pollen diagrams with pollen assemblages plotted against their stratigraphical position through the sediment sequence (Fig. 1). He showed strong similarities in pollen diagrams from a small area, and striking differences between different areas. He was thus able to provide the dimension of time (vegetation's fourth dimension) to the study of past vegetation and forests[2, 3].

Pollen analysis

There are ten basic principles of pollen analysis[1] (see Box 1). The results of a pollen analysis are most commonly presented as a pollen diagram, showing how the percentages of different pollen types vary with depth, and hence age, in the sedimentary sequence (Fig. 1). When many sequences have been studied, their pollen data can be mapped for a particular time interval (e.g. 5 000 years ago) to produce so-called 'isopollen' maps for particular pollen types where the contours represent different pollen values (e.g. 2.5%, 5%, 10%) (Fig. 2)[4]. Alternatively when interest is centred on the directions and rates of tree spreading, so-called 'isochrone' maps can be constructed where the contours represent ages established by radiocarbon dating (e.g. 5 000, 6 000, 7 000 years ago). When the value of a particular pollen type exceeds a certain threshold value it can be interpreted as reflecting the first expansion of that taxon at different sites (Fig. 3)[5]. The first arrival of a taxon is more difficult to assess, because the absence of pollen or macrofossils may not mean a true absence of the taxon in the landscape. Interpretation of pollen-stratigraphical data in a qualitative manner in terms of major past vegetational changes is relatively straightforward[2]. Quantitative interpretation of such data in terms of quantitative estimates of past plant abundances is less straightforward because of the differential production, dispersal, and hence representation of different pollen types. Approaches for quantitative interpretation are currently an area of active research within Europe and elsewhere (e.g. [6, 7]).

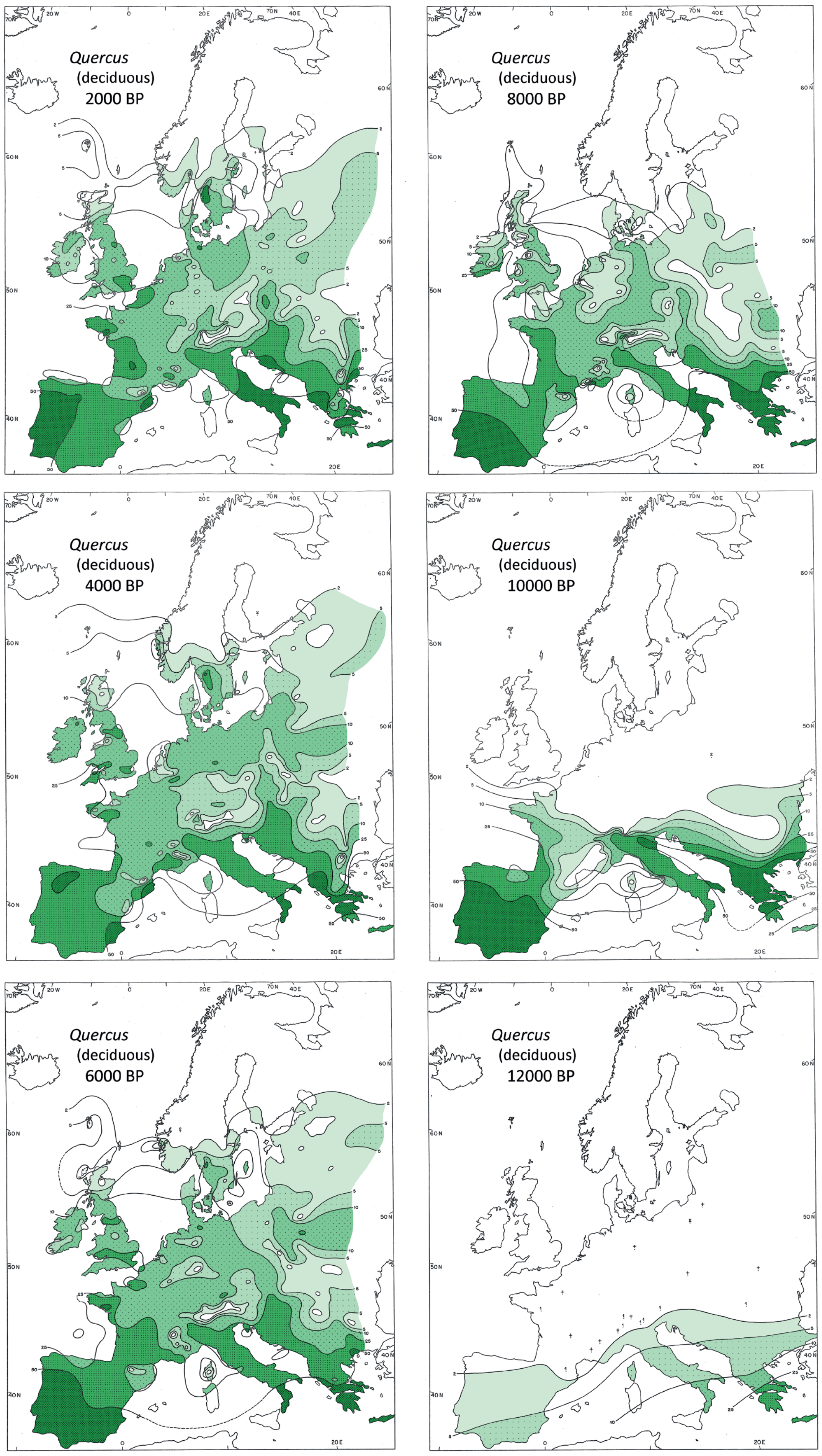
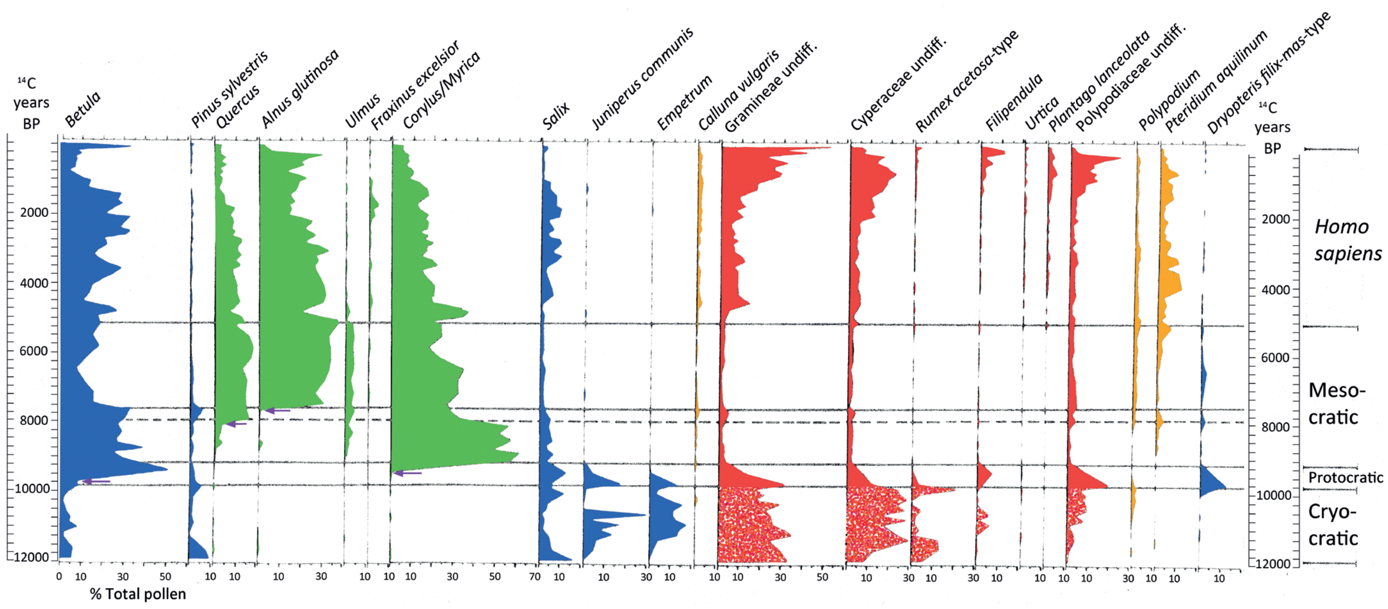


Fig. 2: 'Isopollen' maps of *Quercus* (oak) pollen percentages across Europe for 12 000, 10 000, 8 000, 6 000, 4 000, and 2 000 radiocarbon years before present (BP). Note the progressive northward spread into southern Scandinavia by 6 000 BP and the subsequent contraction at 2 000 BP in Norway. The percentage contours are percentages of total tree and shrub pollen.
(Modified from Huntley and Birks[4])

Fig. 1: Summary pollen diagram from Loch Cill an Aonghais (Argyll), a small lake in south-west Scotland covering the last 12 000 radiocarbon years. The horizontal lines represent partitions of the pollen stratigraphy into pollen-assemblage zones. The vertical axis is radiocarbon (^{14}C) years before present (BP) based on eight radiocarbon dates. The small arrows by the *Betula* (birch), *Quercus* (oak), *Alnus* (alder), and *Corylus/Myrica* (hazel/bog myrtle) indicate when these trees or shrubs are inferred to have first expanded near this site. Cryocratic taxa are coloured red and stippled. These taxa become abundant again in the open conditions of the Homo sapiens phase where they are shown in plain red. Protocratic trees are coloured blue, mesocratic trees are green, oligocratic and telocratic taxa are orange, and taxa associated with human activity and the *Homo sapiens* phase of the Holocene are shown in red. All the pollen and spore percentages are expressed as percentages of the total number of terrestrial pollen and spores counted (generally 500-600 per sample). Pollen analyses by Sylvia M. Peglar.



Box 1: Principles of pollen analysis

i Pollen grains and spores are produced in great abundance by plants

ii A very small fraction of these fulfil their natural reproductive function of transferring the male gamete to the female ovary: the vast majority fall to the ground

iii Pollen and spores decay more or less rapidly, unless the processes of biological decomposition are inhibited by a lack of oxygen, such as in bogs, lakes, and the ocean floor where pollen is preserved

iv Before reaching the ground, pollen is well mixed by atmospheric turbulence, which results in a more or less uniform pollen rain within an area of similar vegetation and landform

v The proportion of each pollen type depends on the number of parent plants and their pollen productivity and dispersal. Hence the pollen rain is a complex function of the composition of the vegetation. A sample of the pollen rain is thus an indirect record of the regional vegetation at that point in space and time

vi Different pollen grains and spores can be identified to various taxonomic levels (e.g. species, genus, family)

vii In vegetated areas pollen is ubiquitous in lake and bog sediments. Very high concentrations (usually around 100 000 cm^{-3}) in the sediment permit efficient analyses and statistically robust results (standard pollen counts are usually ca. 300-1 000 grains per sample).

viii If a sample of the pollen rain is examined from a peat or lake-mud sample of known age (dated by annual layers or radiocarbon dating), the pollen assemblage is an indirect record of the regional and local vegetation surrounding the sampled site at a point of time in the past

ix If pollen assemblages are obtained from several levels through a sediment sequence, they provide a record, admittedly an indirect record, of the regional and local vegetation and their development near the sampled site at various times through the time interval represented by the sedimentary record (Fig. 1)

x If two or more series of pollen assemblage are obtained from several sites, it is possible to study changes in past pollen assemblages and hence in the regional and local vegetation through both time and space (Figs. 2 and 3)

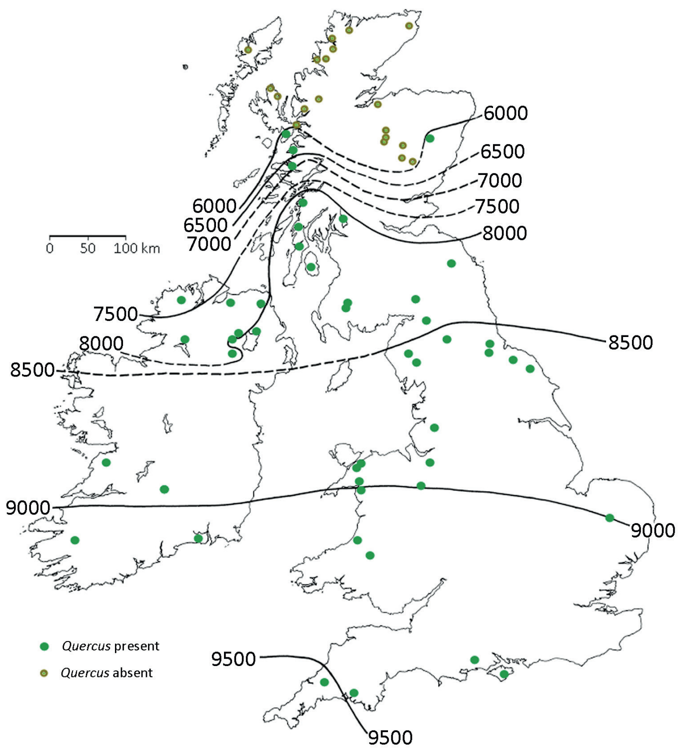


Fig 3: 'Isochrone' map for *Quercus* (oak) in Britain and Ireland showing its progressive rate and/or expansion from the south-west at 9 500 radiocarbon years before present (BP) through England and southern and central Ireland to 8 500 BP and its declining rate as it spreads north into Scotland between 8 000 and 6 000 BP.
(Modified from Birks[5])

Europe's forests prior to the Quaternary ice-ages

The Quaternary period with its multiple glacial stages with ice-sheets and intervening temperate interglacial stages began about 2.6 million years ago. What were European forests like prior to the Quaternary?

Period	Epoch	Age (Million years)
Quaternary	Holocene	0.01
	Pleistocene	2.6
Neogene	Pliocene	5.3
	Miocene	23
Palaeogene	Oligocene	33.9
	Eocene	56
	Palaeocene	66

Table 1. Partial geological time scale. Time is shown in million years with youngest epoch at the top going down to older epochs at the bottom.

Knowledge of the flora and vegetation of the Palaeogene and Neogene ('Tertiary') periods (66-2.6 million years ago, see Table 1 for an outline of the relevant geological time scales) is very fragmentary due to the shortage of fossiliferous sedimentary sequences in Europe[8]. Following the tropical and sub-tropical Palaeocene, Eocene, Oligocene, and Miocene epochs (66-5.3 million years ago) when plants (e.g. *Nipa* palm) found today in the tropical lowlands of the Indo-Malaya region occurred in north-west Europe[9], the European tree flora of the Pliocene epoch (5.3-2.6 million years ago) contained many genera characteristic of modern European forests (e.g. *Quercus* oak, *Carpinus* hornbeam, *Fagus* beech, *Pinus* pine, *Picea* spruce, *Abies* fir) as well as genera growing today in eastern Asia and/or eastern North American (e.g. *Pterocarya* wing-nut, *Liriodendron* tulip-tree, *Tsuga* hemlock, *Liquidambar* sweetgum, *Nyssa* blackgum, *Sequoia* redwood, *Taxodium* cypress, *Magnolia* magnolia, *Carya* hickory, *Clethra* pepper-bush, *Engelhardia*, *Aesculus* chestnut)[9, 10]. These trees belong to the so-called **Arcto-Tertiary geoflora** that in the Neogene existed widely in the Northern Hemisphere across North America, Europe, and Asia. This geoflora was first defined by J.S. Gardner and C. Ettinghausen in 1869. The successive loss of these taxa during the Pliocene epoch and the early Pleistocene of the Quaternary and their restriction today to two almost opposite areas of the globe (eastern Asia and eastern North America) is explained by the hypothesis explicitly presented in the 1850s by the American botanist Asa Gray (1810-88). The cool phases within the late Pliocene epoch and the subsequent Pleistocene continental glaciations, combined with the west-east chains of glaciated mountains (e.g. Pyrenees, Alps, Carpathians, Caucasus mountains) and the Mediterranean Sea provided barriers to the southward retreat of many of the Arcto-Tertiary geoflora resulting in their progressive extinction in Europe. In contrast, the mountain chains and valleys of south-eastern Asia (e.g. Yunnan) and North America (e.g. Appalachians, Rocky Mountains) run north-west to south-east or north to south reaching low latitudes without sea barriers, thereby permitting temperate and warm temperate trees to spread southward along unglaciated areas or valley corridors in cold stages and to spread northward during temperate intervals. As a result of the west-east barriers and the many relatively cold stages in the late Pliocene and early Pleistocene, Europe lost many trees or their close relatives that today are found in the warm-temperate-subtropical 'evergreen forest' of south-eastern China[11]. These were largely replaced by trees of the temperate 'mixed **mesophytic** forest'. Many taxa had already disappeared at the beginning of the Quaternary (e.g. *Liquidambar, Meliosma, Pseudolarix* false larch, *Stewartia*), while others survived longer (e.g. *Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron* cork tree, *Tsuga, Carya*) to vanish finally from Europe during the course of the early- or mid-Quaternary[9, 11].

Europe's forests in the Quaternary period

The Quaternary period (last 2.6 million years) witnessed very marked and widespread climatic and environmental changes[12]. Large terrestrial ice-sheets started to form in the Northern Hemisphere about 2.75 million years ago, resulting in multiple (at least 50) glacial-interglacial cycles driven by secular variations in insolation as a result of periodic fluctuations in the Earth's orbit around the sun. Glacial-stage conditions account for 80% of the Quaternary whereas the remaining 20% consists of shorter interglacial stages during which conditions were similar to, or slightly warmer than, the present day[12]. During the glacial stages, environmental conditions were very different from the present interglacial (Holocene or post-glacial plus the recent Anthropocene) in which we live today. Much of the region north of 40°N was covered by large terrestrial ice-sheets and widespread permafrost with temperatures possibly 10-25 ° C lower than present. High aridity and temperature 2-5 ° C lower than today were features of low-latitude areas. Global atmospheric CO_2 concentrations were as low as 180 ppm during glacial stages, rising to pre-industrial levels of 280 ppm in interglacial stages. Given these extreme conditions in the glacial stages that cover 80% of the last 2.6 million years, an obvious question[12] is how did European forest trees survive these repeated long glacial-stage conditions and where did they grow in the glacial stages?

The evidence we have suggests that many European trees survived the last glacial maximum (LGM) in relatively narrow refugial elevational belts (ca. 500-800m) in the mountains of southern Europe (including the Caucasus) and possibly in parts of western Asia[13]. These belts lay between lowland xeric steppe-like vegetation too dry for tree growth and high-elevation tundra-like vegetation, or permanent snow or ice, too cold for tree growth. Such mid-elevation belts of trees can be seen today in the Andes, American Rockies, the Californian Sierra Nevada, the Pamir, parts of the Sino-Himalayan region, and the Tien Shan in Kazakhstan[12]. Trees may also have occurred scattered in locally moist sites (water seepages, ravines), so-called '**cryptic**' or '**micro' refugia** in Europe during the LGM as they do today on the Tibetan Plateau in Sichuan and Qinghai, in the Zagros mountains of Iran, and in parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan[12]. There is increasing evidence from macrofossils and charcoal remains in central, eastern, and north-eastern Europe that conifer trees such as *Pinus, Picea*, and *Larix* larch may have grown locally in such microrefugia during the LGM, along with *Betula* birch, *Salix* willow, and possibly *Alnus* alder, *Populus* aspen, and *Ulmus* elm, as far north as the north-eastern edge of the great Fennoscandian ice-sheet in Russia at 60°N ([12], but see [14] for a contrasting view).

Europe's forests during Quaternary interglacial stages

Pollen analysis and macrofossil studies reveal that in north-western and central Europe[15] there is strikingly similar vegetation development from the end of a glacial stage through the ensuing interglacial (about 10 000-15 000 years duration) and into the next glacial stage. Although the species and their relative abundances may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johannes Iversen recognised in 1958[16] an interglacial cycle consisting of four or five ecological phases (Box 2 and Fig. 4)[17, 18]. The *cryocratic* phase represents the cold and dry, often glacial, stage with sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal herbs growing on skeletal mineral soils, frequently disturbed by ground-ice activities. Trees are absent, except in specialised refugia.

At the onset of an interglacial, temperature and moisture rise and the *protocratic* phase begins. Base-demanding shade-intolerant herbs, shrubs, and trees (e.g. *Betula, Salix, Populus, Pinus, Juniperus* juniper, *Sorbus aucuparia* rowan) immigrate into formerly glaciated areas and expand to form a mosaic of grassland, scrub, and open woodland growing on unleached, fertile soils rich in nitrogen and phosphorus and with a low humus content (Fig. 1). The *mesocratic* phase is characterised by the development of temperate deciduous forests of *Quercus, Ulmus, Tilia* lime, *Corylus* hazel, *Fraxinus* ash, and *Alnus* on fertile brown-earth soils (Fig. 1). Shade-intolerant herbs and shrubs are rare as a result of competition and habitat loss, except in openings caused by fire, wind-throw, and, possibly, grazing mega-fauna[19]. The next phase, the oligocratic phase, comprises open conifer-dominated woods (*Pinus, Picea, Abies*), ericaceous heaths, and bog vegetation growing on infertile (low available phosphorus[18]) humus-rich podsols and peats. Climatic deterioration (temperature decreases, reduced moisture, etc.) occur in the final telocratic phase and, most especially, at the onset of the next glacial *cryocratic* phase as forests decline, frost action and cryoturbation destroy the leached infertile acid soils, and herbs expand on the newly exposed mineral soils. The telocratic forest vegetation is very similar to the *oligocratic* phase except that as the climate cools towards the end of the interglacial, warmth-demanding and or frost-sensitive trees and shrubs (e.g. *Tilia, Ilex, Hedera*) decline. These ecological phases within an interglacial are not synchronous between sites because the onset of a phase such as the *oligocratic* phase may depend on local site features such as bedrock geology, topography, climate, and land-use.

The characteristic trees of the interglacial phases differ in their reproductive and population biology and ecological and competitive tolerances[17, 20, 21]. *Protocratic* trees have high reproduction rates, low competitive tolerances, high rates of population increase, and display 'pioneer' and 'exploitation' traits[17]. *Mesocratic* trees have low reproductive rates, high competitive tolerances, medium-low rates of population increase, arbuscular phosphorus-scavenging mycorrhiza, and 'late-successional', 'competitive', and 'saturation' traits [17]. *Oligocratic* and *telocratic* trees have medium reproductive rates, high competitive tolerances, medium-low rates of population increase, **ectomycorrhiza** with a phosphorus-mining strategy, and 'cold-stress tolerant' and 'adversity' traits[17].

Within these three broad groups of *protocratic, mesocratic,* and *oligocratic* and *telocratic* plants, the actual floristic and forest composition varies from interglacial to interglacial in north-western and central Europe[17]. Factors such as location of refugia in the *cryocratic* phase, rates of spreading, distances over which spread occurred, competition, predation, genotypic variation, and chance as it affects survival, dispersal, and establishment may all have contributed to the observed differences in interglacial forest patterns[17]. Similar cycles occurred in southern Europe, yet with substantial differences in comparison to central and north-western Europe[10, 11, 22]. Due to warmer conditions, European tree species persisted locally, although strongly reduced, in the steppe-like environments of the glacial stages. This corresponds to the *cryocratic* phase in central and northern Europe. At the onset of an interglacial, corresponding to the *protocratic* phase in central and north-western Europe, temperate taxa (e.g. deciduous *Quercus, Ulmus, Ostrya* hop-hornbeam, *Carpinus*) form open forests together with evergreen broad-leaved trees (e.g. *Quercus ilex* holm oak, *Olea europaea* olive) and mediterranean shrubs (e.g. *Pistacia* pistachio), while boreal and steppe vegetation declines (e.g. *Betula, Juniperus, Artemisia* wormwood, Chenopodiaceae goosefoot)[11, 22, 23]. In the following phase during the mid-interglacial, corresponding to the *mesocratic* phase in central and north-western Europe, warm-temperate and Mediterranean conifers (e.g. *Abies, Pinus*) expand into the broad-leaved deciduous and broad-leaved evergreen forests and arboreal cover increases, probably in response to rising moisture availability. Towards the end of the interglacials, corresponding to the oligocratic phase in north-western and central Europe, moisture-loving taxa such as *Fagus, Alnus,* and *Abies* gradually replace Mediterranean evergreen broad-leaved trees, while broad-leaved deciduous trees remain important[11, 22, 23]. Finally, forest cover declines and steppe-like environments expand during the climatic deterioration at the transition from the interglacial to the next glacial (temperature decreases, reduced moisture), corresponding to the *telocratic* phase. There is an apparent order within interglacial forest patterns when viewed at the broad-scale of an entire interglacial cycle of 10 000-15 000 years, whereas within each phase of an interglacial (ca. 5 000 years) there is often great variation between interglacials, hence the ability of pollen stratigraphy to differentiate between many of the different interglacials[17].

Europe's forests in the Holocene (11 700 years ago-today)

The mesocratic phase in the Holocene interglacial stage was greatly modified about 5 000-6 000 years ago by the onset of forest clearance and prehistoric shifting cultivation and livestock farming (Fig. 1). This new phase, unique to the Holocene is called the *Homo sapiens* phase (see Box 2)[17]. There was a steep fall in *Ulmus* pollen values (Fig. 1), probably a result of an interaction between prehistoric human activities and a tree pathogen, with elm pollen values halving within 5 years at a site in southern England[24]. Similarly, 5 000-6 000 years ago *Abies* disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive Neolithic disturbance by fire and by browsing[25, 26]. As with *Ulmus* in England, *Abies* collapses were rapid, with pollen values of *Abies* halving within 13 and 22 years at sites in Italy[27] and Italian Switzerland[28], respectively.

In some areas of central and north-west Europe, forest clearance and subsequent dereliction of clearings may have facilitated local colonisation and expansion of new immigrants such as *Fagus sylvatica* European beech, *Picea abies* Norway spruce, and possibly *Carpinus betulus* European hornbeam[4]. While the establishment of *Fagus sylvatica* during **Mesolithic** times followed climate change (cooling and a moisture increase) in southern and southern-central Europe[29], it is possible that the rapid spread of *Fagus* across central Europe in the last 4 000-5 000 years[4] may have only been facilitated by the creation of abundant, large clearings within *Tilia*- or *Quercus*-dominated forests on well-drained soils. In some areas mixed *Fagus-Ilex* holly-*Quercus* forests developed whereas in other areas there was a rapid change from *Tilia*- or *Quercus*-dominance to *Fagus*-dominance[17]. These changes commonly occurred after an extensive phase of human activity involving clearance and grazing followed by the abandonment of cleared and cultivated areas. This abandonment may have occurred as a result of local population collapse following, for example, climate change, emigration, or over-exploitation of environmental resources[30].

Other types of secondary woodland developed in areas beyond the natural geographical range of *Fagus*, for example woods of pure *Fraxinus excelsior* European ash, *Quercus* spp., *Taxus baccata* English yew, *Betula* spp., or *Ilex aquifolium* common holly became established on particular soil types following abandonment of cleared or cultivated areas, relaxation in grazing pressure, or reduction in fire frequency[17].

The westward, northward, and southward spread and expansion of *Picea abies* through Finland, Sweden, and Norway over the last 6 000-7 000 years[4, 31] may be a contemporaneous response to subtle step-wise climate change, a delayed migration unrelated to simple climate change, a response to forest disturbance creating gaps for colonisation, or a combination of these factors[32]. Whatever its causes, the invasion of *Picea* into northern and central Fennoscandia over the last 6 000-7 000 years resulted in major changes in forest composition and structure and in soil conditions, with widespread accumulation of mor humus, soil leaching, and **podsolisation** and changes in the natural fire regime within the boreal forest[15, 33].

Box 2: Glacial-interglacial phases in north-west Europe

The glacial-interglacial cycle showing the broad changes in biomass, soil, and temperature that take place during a glacial (cryocratic) stage and associated interglacial stage. The phases of the interglacial (protocratic, mesocratic, oligocratic, and telocratic) are shown along with the dominant soil features.

Cryocratic:
- glacial stage
- sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal plants
- skeletal mineral soils

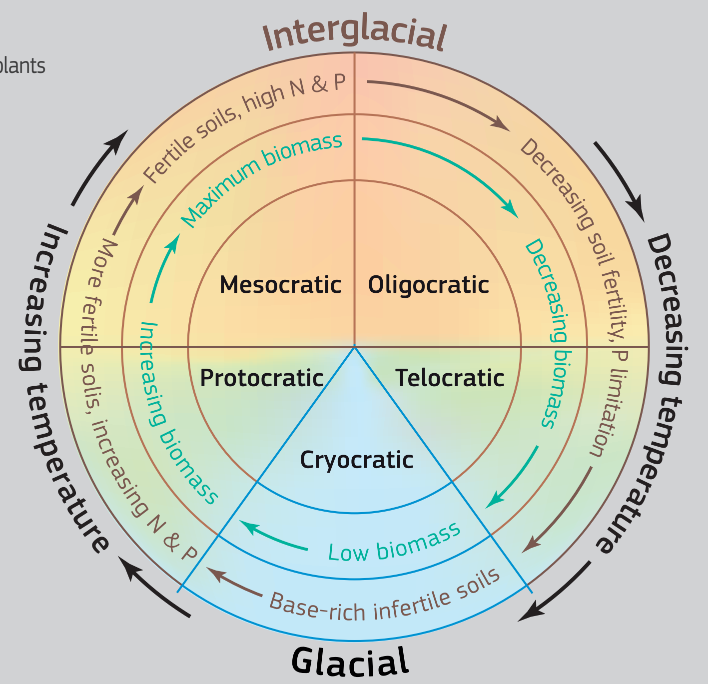
Protocratic:
- early interglacial stage
- rich assemblages of herbs, shrubs, and trees (birch, pine, willow)
- unleached fertile soils

Mesocratic:
- mid interglacial stage
- temperate deciduous forests
- fertile brown-earth soils

Oligocratic & Telocratic:
- late interglacial stage
- open conifer (spruce, pine), ericaceous heaths, bogs
- infertile, humus-rich podsols and peats

Unique to the Holocene

Homo sapiens:
- mid-late Holocene (6 000 years ago-present)
- forest clearance, agriculture
- range of soil types, often fertilised



(Modified from Birks and Birks[18])

Box 3: Palaeo-model comparison: past, present and future Mediterranean vegetation

Simulation of future vegetation dynamics at Lago di Massaciuccoli, a coastal lake in Tuscany (central Italy), with a dynamic vegetation model (LANDCLIM) for different climatic conditions (today vs. warming) and levels of disturbance (low vs. moderate). The mid- to late-Holocene sedimentary pollen record of Lago di Massaciuccoli is used to validate the model, in particular LANDCLIM is able to simulate extinct vegetation types which were growing in the past at the site before anthropogenic disturbance became excessive.

a) Present-day (1950-2000 AD) mean monthly temperature (±1 standard deviation) and average total monthly precipitation at Lago di Massaciuccoli close to Pisa (Tuscany).

b) Map of Italy and Switzerland with Lago di Massaciuccoli denoted by a black star, red star shows position of Gorgo Basso in southern Sicily (Fig 4).

c) Future (2071-2100 AD) mean monthly temperature and precipitation projected by a regional climate model (SMHI) for Lago di Massaciuccoli.

d) and e) Vegetation simulated at Lago di Massaciuccoli with LANDCLIM, a dynamic vegetation model with d) present climate and future climate e). All vegetation models were initialised with the same present-day climate scenario and moderate disturbance before 2010.

f) Holocene pollen percentages of upland trees and shrubs at Lago di Massaciuccoli.

Simulations of today's vegetation under low disturbance shows *Abies alba* co-dominance with *Quercus ilex* (see right image) in the Mediterranean forest. This vegetation type disappeared during the late Holocene most likely in response to excessive anthropogenic burning and land use[25]. In agreement, simulations show the disappearance of this vegetation type under current climate with moderate land use. Future climate and vegetation conditions at Lago di Massaciuccoli are comparable to present climate and vegetation conditions at Gorgo Basso, southern Sicily (Fig 5). With low land use, evergreen oak forest will prevail[16], while under moderate land use forests will be reduced and maquis (low biomass) will expand.

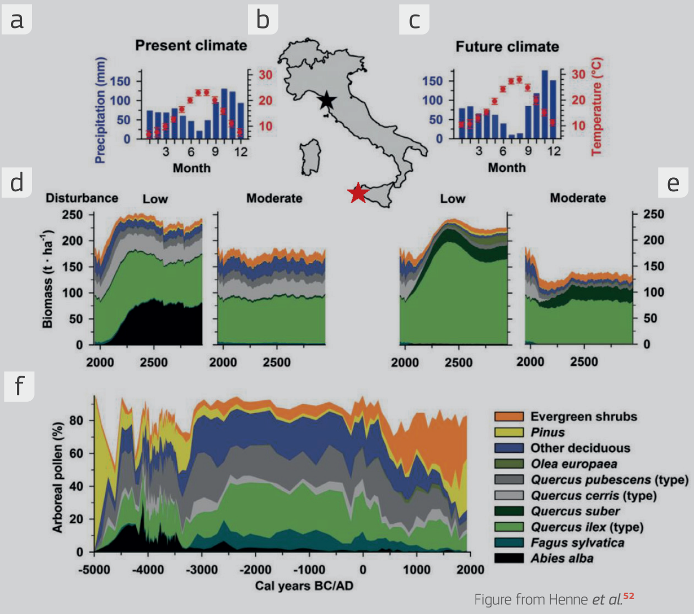


Figure from Henne *et al.*[52]

Spontaneous regeneration of *Abies alba* and *Quercus ilex* in a **cryptic** Mediterranean stand in lowland Tuscany.

Fig. 4: Xeric maquis and cultivated land north of Gorgo Basso, a small lake in southern coastal Sicily. This sclerophyllous vegetation type expanded 2700-2000 years ago with Greek and Roman colonisation involving regular vegetation burning, pastoral and arable farming[37].

Fig. 5: Dense evergreen oak forest (*Quercus ilex*) south of Gorgo Basso. This vegetation type is representative of natural conditions in coastal Sicily prior to human-induced creation of maquis vegetation (Fig. 4). Forest vegetation survived on rocky calcareous slopes less suited for agriculture.

In general, disturbance-sensitive taxa such as *Tilia*, *Ulmus*, *Fraxinus*, *Acer* maple, *Abies*, and *Hedera* ivy declined while disturbance-resistant taxa such as *Quercus*, *Ostrya*, *Corylus*, *Betula*, *Alnus*, *Salix*, *Fagus* (re-sprouters), and *Picea* (non-palatable) expanded[34]. *Quercus*, *Fagus*, and *Picea* were also favoured by humans for their valuable acorns or timber, ultimately forming monospecific forests[25, 35]. Continued forest clearances and agriculture, interspersed by periods of abandonment and secondary regeneration, occurred as the result of the development and expansion of more permanent land-use practices (e.g. animal husbandry, ploughing, crop cultivation, woodland management) during the late Neolithic, Bronze Age, Iron Age, Roman, Viking, Medieval, and recent times. Forests initially became more open, and wood- and scrub-pasture and hazel coppice expanded. However, increased human interference including regular burning[36] led ultimately to the widespread deforestation of much of Europe and the development of extensive pastures of 'commons', fields, heaths, maquis, and settlements (Figs. 4 and 5). This process was particularly intense in the lowlands of Mediterranean Europe, where practically no unplanted forest environments survive (e.g.[27, 37]). Almost all extensive and naturally forested areas surviving today have been extensively managed by selective silviculture over many centuries[38, 39].

Why is European forest history important to modern ecologists?

What 'lessons from the past' can be learnt from the ever-changing composition, structure, and extent of forests in Europe? We see that European forests have been changing since the Palaeogene, with progressive extinction from Europe of trees of the so-called Arcto-Tertiary geoflora in the Pliocene and early Pleistocene[9, 10]. The repeated glacial-interglacial cycles[15, 17] that are so characteristic of the Quaternary (Pleistocene, Holocene) have resulted in a continuous dynamic of tree survival in refugia during glacial stages and rapid spread and expansion and unique tree combinations in the different interglacial stages[13, 17]. Human impact with forest clearance and agriculture (Fig. 4, maquis and Fig. 5, *Quercus ilex* forest) are unique to the Holocene, the so-called *Homo sapiens* phase (see Box 2)[17]. What emerges from the many palaeoecological studies (mainly based on pollen analysis but increasingly strengthened by macrofossil studies) is continual change at time scales of millions, thousands, and hundreds of years. Forests develop when certain plant species become abundant and dominant at specific areas under particular environmental conditions[40]. These forests may change gradually or abruptly when the dominant trees are replaced by other trees, usually in response to extrinsic environmental change[41] or major disturbances (e.g. forest pathogens, fire, human activity)[17]. Few major terrestrial forest systems have existed for more than 10000 years and most are considerably younger, some developing only within the last few centuries[38-40]. Future forest systems are thus inevitably uncertain and historically contingent. Given the richness of forest-tree responses during the Quaternary with all its climatic shifts[10, 13, 15, 17], many novel future responses, outcomes, and ecological surprises are certainly possible[42-46].

Assessing whether current forest systems are sustainable in the face of future global change is aided by considering the range of environmental variation that these systems have experienced in the past and by reconstructing the environmental conditions under which these systems were initiated and developed[40]. A narrow time window (e.g. 200-300 years) underestimates the range of variation within which a forest system is sustainable, and this underestimates the risk of major disruption of the system by environmental change[40]. Longer time periods (e.g. 1000-2000 years) inevitably increase the inherent range of natural variation in the earth system[40]. Most systems disappear, as shown by the palaeoecological record, when the time window extends to 10000-15000 due to major changes in the Earth's climate system due to orbital forcing[9]. The palaeoecological record can pinpoint the time of origination of particular forest systems (e.g. [30, 38]) and can, by inference in some cases, indicate the specific environmental changes that led to the development of the system and the range of environmental variation under which the system maintained itself in the past[40]. Such information, only obtainable from the palaeoecological record, can thus help to identify critical environmental thresholds beyond which specific modern forest systems can no longer be sustained[47, 48].

The palaeoecological record for European forests provides several additional insights and important lessons from the past[40]. First, all existing forest systems have a finite time limit to growing in the places where they occur and all have been preceded by ecosystems (not necessarily forest systems) that differ in composition, structure, plant-functional traits, and ecosystem properties[40]. Second, similar forest ecosystems, as defined by their dominant species have developed in different places and at different times[17, 40]. Third, similar systems had different antecedents in different places. Thus apparently similar systems may have different properties owing to different histories and to legacy effects of different antecedents[40]. Fourth, several different systems arose at approximately the same time in different places, presumably in response to regional- or global-scale shifts in atmospheric circulation involving climatic shifts that led to widespread synchronous transformations of ecosystems[40, 49, 50]. This pattern is not, however, universal but rapid regime-shifts in the earth system may be accompanied by widespread ecosystem changes in diverse regions[40, 41]. Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and forest systems existed in the past that have no modern counterparts ('analogues')[45, 46]. Examples include the former abundance of *Corylus avellana* in the early Holocene across much of north-west Europe[4, 17] and the importance of *Abies alba* in southern Europe in the mid-Holocene (See Box 3)[25, 26].

Palaeoecologists look to the past whereas global-change ecologists look to the future, but both rely solely on their understanding of modern ecosystems and ecological processes as a basis for past reconstructions or future predictions. Palaeoecologists apply the concept that "the present is the key to the past" whereas global-change ecologists project this forward and use "the present is the key to the future". But the present is only one time-slice in the last 11700 years since the last glacial stage. A critical question is thus are today's ecosystems and climate representative of tree and ecosystem-climate relationships under past or future climate change? Are they robust to climate conditions beyond modern states? Are species ranges in equilibrium with environmental factors such as climate[50] or have the realised environmental niches of species been significantly altered by climate-change or millennial-long land-use activities[51]? These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present-day observations[47]. A promising novel approach is to combine dynamic eco-physiological models with palaeoecological evidence to produce palaeo-validated scenarios of future vegetation dynamics under global-change conditions[52, 53].

The dynamic nature and the often non-analogue character of European forests in the time-span of the Holocene or even the last 5000 years raises critical questions about appropriate targets ('baselines') for restoration efforts. Palaeoecological studies have revealed major human imprints on many, if not all, systems in Europe[17, 34] and have shown that secular climate change has kept many targets moving at centennial to millennial time-scales[9, 17, 54]. Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades [34]. Restoration efforts should aim to conserve or restore historical systems if possible, but more importantly, to design, create, and manage emerging novel ecosystems to ensure high biodiversity and a supply of ecosystem goods and services in the future[54].

The palaeoecological record of European tree and forest history is a rich and largely untapped record of ecological dynamics over a wide range of time-scales. As Karl Flessa and Steve Jackson[55] discuss, this record is a long-term ecological observatory where ecological responses to past climate change and the ecological legacies of societal activities can be deciphered, quantified, and used as a key to "understanding the biotic effects of future environmental change"[55]. There is very much still to be learnt about past European forests using the vast amount of palaeoecological data available in Europe[4, 15, 17, 25, 29, 36, 56].

Acknowledgements

We are very grateful to Cathy Jenks for preparing this text and figures in a very short time and for her meticulous editing.

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Please, cite as:

Birks, H. J. B., Tinner, W., 2016. **Past forests of Europe**. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. e010c45+